A COMPARISON OF THE SHOULDER BONES AND MUSCLES WITH THE PELVIC BONES AND MUSCLES. By Professor Humphry, (Pl. III.)

Professor Flower's paper "On the Correspondence between the parts composing the Shoulder and the Pelvic Girdles of the Mammalia," contained in the last Number of this Journal, has induced me to reconsider the subject; and the conclusions at which I arrive do not entirely accord with those of Professor Flower, or with those to which, as he intimates, I myself in some degree formerly inclined. The fact of its being a trite subject, which has been handled by many and able anatomists, proves that it is a difficult one, and therefore interesting; and it is moreover interesting because several of the great principles of animal construction, that is, of morphology and homology, are involved in it. It is quite clear that the fore and the hind limbs are in the main alike; yet a certain amount of dissimilarity pervades every part of them in every animal, adapts each to its special purposes, and is therefore least at the middle, and most marked in the proximal and distal parts of the limbs. The same remarks apply to the limbs in the several members of the vertebrate division. Throughout, variety is grafted upon uniformity. The object of the variety is conformity to the special purposes of the limb, and adaptability to the varieties—that is, the peculiarities—of the several animals. Unfailing in result and regulated by some utterly unknown force, it offers innumerable problems to the homologist, many of which are difficult and some perhaps impossible of solution. When we remember how hard it is correctly to compare the several processes in two distant vertebræ of the same spinal column, although we have the aid afforded by all the gradations presented in the intervening vertebræ, we cannot be surprised that a successful comparison of two limbs placed at opposite ends of the trunk, with different movements and functions, and unconnected by intermediate gradations, has not yet been made. The difficulty of instituting a correct homological comparison is augmented by the fact that the deviations from one another, or of both from a simple and common original, are

very early elements in development, are owing indeed to inherent qualities in the two limbs which are operating from the very beginning of each, and which are working on—and that is a very important point to bear in mind in all developmental and homological investigations—are working on with reference to adaptation to future conditions, and so are prophetic, as it were, of them. For instance, if an alteration in the direction of the circulating current is to take place at a late period of development, the preparation for it is going on throughout the earlier periods of embryonic life; the several parts are forming to effect, and to adapt themselves to, the coming event; and, in the case of the limbs, if rotation or other changes in the hind limb are to occur, differing from those in the fore limb, the developmental processes will, from the earliest period, be directed with reference to them, and will prepare the several parts for them—will prepare, that is, the individual parts for harmonious corporation with the general modification. It may be that they will do so in such a manner as to destroy exact correspondence between the limbs, not only apparently but really, and so render futile the attempt to make an exact homological comparison. If a given muscle passes in one limb on one side, and in another limb on the other side, of a certain muscle or bone, it cannot be said to be strictly homologous in the two limbs, however close its correspondence in other respects may be. Such displacements or variations in the position of corresponding muscles are by no means uncommon. We must be content, therefore, in some cases with establishing a general correspondence, and avoid the error of endeavouring to work out a closer homological relationship than actually exists. These remarks will find their application in the following comparison.

It may be regarded as now sufficiently established, that the extensor and flexor surfaces of the two limbs, of the parts of them, at least, which project from the trunk, answer respectively to one another, and that the radial edge of the fore limb, including the pollex, the outer condyle, and the outer tubercle of the humerus, corresponds with the tibial edge of the hind limb, including the hallux, the inner condyle, and the inner or lesser trochanter of the femur; and, accordingly, that the ulnar

edge of the fore limb, including the inner condyle and inner tubercle of the humerus, corresponds with the fibular edge of the hind limb, including the outer condyle and the outer or greater trochanter of the femur. We may consider that the extensor surfaces of the two limbs form essentially and originally parts of the dorsal plane of the animal, or are an extension of it, and that the flexor surfaces are parts of the ventral plane; and most anatomists accept the view that the two limbs may be considered to have undergone a partial rotation in opposite directions, which has had the effect of throwing the extensor surface of the hind limb forwards, and the extensor surface of the elbow and a considerable part of the fore limb backwards. Many of the apparent discrepancies between the two limbs are thus explained[1].

It is obvious that this rotation does not affect the limbs of all animals alike. In many reptiles it affects them but little; and these animals furnish therefore much aid in the comparison of the limbs. Moreover, it does not affect all parts of each limb to an equal extent. The distal part of the fore limb in some mammals and in birds retains the primitive direction of its surfaces; and in most mammals it undergoes a rotation in a direction opposite to that of the rest of the limb, and like that of the hind limb; for its dorsal surface is, like that of the hind foot, directed forwards, and its ventral surface backwards. The Bat offers an interesting example of the rotation of an entire limb in a contrary direction to that which is usual, the whole flexor or ventral aspect of its hind limb being turned forwards.

The question arises, is this rotation of the limbs participated in by their respective trunk-segments or girdles, or by any parts of them? With regard to the lower portions of these girdles—the coracoid elements in the shoulder, and the ischiatic and pubic elements in the pelvis—I am not aware that such rotation has ever been supposed, and the evidence is greatly against it. It is pretty clear that the respective external and internal surfaces of these elements in the two girdles answer to one another, and to the external and internal planes of the visceral laminæ in which they are formed. This, it must be admitted, is strong presumptive evidence against any rotation

[1] See my *Observations on the Limbs of Vertebrate Animals*, p. 16.

of the superior elements of the girdles (the scapular and iliac parts). The several parts of each girdle are, in their early and their cartilaginous conditions—and indeed to a great extent throughout life—in one piece, unsegmented, the distinction being caused by the formation of independent centres of ossifications, which after a time become blended, rather than upon any real separation or segmentation. This at least is the case except where the coracoid becomes separate. It is therefore difficult to suppose that the scapula and ilium can undergo a rotation which is not participated in by the coracoid and ischium. Moreover, it is pretty certain that the external surfaces of the lower parts of these two—the articular surfaces and the spaces just above the articular surfaces upon which the prolongations of the triceps brachii and of the rectus femoris extend—answer to one another.

The only question, then, which remains—and this I believe, though it has not been quite clearly stated, is the only one which has really been raised—is whether a rotation in opposite directions takes place in the upper parts of the scapula and ilium, turning that which was the dorsal surface of the blade of the scapula backwards, or backwards and inwards, and that which was the dorsal surface of the blade of the ilium forwards; so that the dorsal aspect of the scapular blade with its muscles answers homologically to the surface of the ilium which is covered by the iliac muscle and that muscle, while the subscapular aspect of the scapular and the subscapularis muscle are homologous with the gluteal aspect of the ilium and certain of the glutei muscles.

Now I am not aware that there is any example of a corresponding twist in the length—that is, between the two ends—of any of the bones of the limbs, though something of the kind has been assumed with regard to the humerus by M. Martins of Montpellier. The rotation appears in each instance to affect one or more entire bones, and not to be caused by a twist in any one. Thus the entire radius is rotated upon the humerus and the ulna, and the entire humerus is rotated upon the scapula. It seems less probable that a bone, or part of a bone, formed in the wall of the trunk and connected on all sides with surrounding adherent tissues, should undergo a rotation similar to that

which has been supposed. I think, moreover, the peculiarities in the two limbs may be explained and harmonized without resorting to any such explanation.

In the paper already referred to, Professor Flower truly observes that "in every mammal both scapula and ilium may be resolved into a bar or rod of three-sided or prismatic form" with the two extremities placed dorsally and ventrally. "The dorsal or upper extremity is capped by the supra-scapular epiphysis in the shoulder-girdle, and by the corresponding supra-iliac epiphysis in the pelvic girdle. The ventral or inferior extremity enters into the formation of the glenoid or the cotyloid articular cavity, as the case may be, and joins with the *coracoid* or the *ischial* element of the girdle." But Professor Flower goes on to make a distinction between the direction of the borders and surfaces of this prism in the ideal and the human scapula and pelvis, a distinction based upon the theory of the rotation of these parts, in which I am unable to concur; for, as just stated, the ideal and the human girdles, and consequently the ideal and the human scapula and pelvis, appear to me to correspond very closely.

Take the ilium of an Echidna (fig. 1) or a Kangaroo, in both of which—and indeed in many other instances—the prismatic form is well presented. Of the three margins or borders one is external and descends to, or nearly to, the upper edge of the cotyloid cavity. It separates the antero-external surface which is covered by the *iliacus internus* muscle from the postero-external surface, which is covered by the *glutei*. It represents therefore the blade and fore part of the crest of the ilium. Its position and appearance and relation to the *iliacus internus*, which Mr Mivart and others on good grounds regard as the homologue of the *supra-spinatus*, are strongly suggestive of its answering to the spine of the scapula, and we shall find other reasons confirmatory of that view. The anterior margin or border is continuous with the linea ilio-pectinea of the os pubis, separates the antero-external or iliacus surface from the internal or ventral surface and is the anterior, or inner, or ilio-pectineal edge of the ilium. The hinder margin or border separates the postero-external or gluteal surface from the internal or ventral, and represents the hinder or sciatic edge of the ilium. If I am

right in believing, as I think I can show that I am, that the external ridge is the representative of the iliac blade and fore part of the crest, and that it answers to the spine of the scapula, then it follows that the anterior or ilio-pectineal ridge answers to the supra- or rather pre-spinal portion and margin of the scapula, and that the posterior or sacro-sciatic ridge answers to the back part and the posterior border of the scapula. It follows also that the ventral surface of the ilium, that is the surface behind the ilio-pectineal line, including the space for articulation with the sacrum, corresponds with the ventral or subscapular surface of the scapula; and the dorsum or gluteal region of the ilium corresponds with the infra- or rather post-spinal region of the dorsum of the scapula, *i.e.*, the part behind the spine and extending over the hinder aspect of the spine.

In the Kangaroo and Echidna the prismatic form of the ilium is well preserved; the three ridges are of nearly equal prominence, and the three surfaces are of nearly equal size. This is also the case in some rodents, as the Beaver (fig. 2). In other instances the ridges are unequally developed, and the surfaces consequently are of unequal size. In the Hare (fig. 3) and Rabbit the ilium is comparatively flat and broad in consequence of the outgrowth of the anterior and posterior ridges, while the external ridge is scarcely perceptible. In this instance the iliacus internus lies upon the outer surface of the anterior or ilio-pectineal border of the ilium, rather than upon the inner surface of the outer border; and the ilium unmistakably resembles the scapula in those animals in which the spine is suppressed, as the Horse (fig. 5). This is however rather exceptional. In most mammals the anterior ridge is but little developed, and is recognized only as the 'ilio-pectineal line' or 'brim' upon the inner surface of the ilium, separating the true from the false pelvis. The external ridge becomes developed in very varying degrees. Still suppressed (the ilium preserving much of its primitive form) in carnivora, its upper margin runs out into an overhanging crest in the Wombat and in ruminants; whereas in pachyderms, monkeys and Man it grows out in its whole length forming the part of the blade and crest of the ilium which lies above and anterior to the ilio-pectineal line and the articulating surface for the sacrum. The iliacus

internus now rests upon the inner aspect of this broad ridge, and the conformation of the ilium corresponds closely with that of the scapula of the Echidna.

The posterior or sacro-sciatic ridge—which bears relations to the ischium and to the large nerves and blood-vessels of the hind limb corresponding to the relations which the hinder border of the scapula bears to the coracoid in ovipara, and to the large nerves and blood-vessels of the fore limb—grows out in varying degrees; and its upper part is often produced backwards into a 'posterior spine' overhanging the sacro-sciatic notch and resembling the 'posterior angle' of the scapula.

Whatever value may be attached to the disposition of the nutritious foramina in the two bones—and it cannot be considered to be unimportant—it certainly favours, in rather a remarkable manner, the view I have taken. These foramina will be found pretty regularly, in man at any rate, in five sets in each bone. *First*, in the ilium on the anterior aspect of the iliac blade near the linea-ilio-pectinea, and in the scapula on the anterior aspect of the spine near the anterior or pre-spinal ridge: *secondly*, in the ilium on the posterior or gluteal aspect of the blade nearly opposite the preceding, and in the scapula on the posterior aspect of the spine in a corresponding situation. *Thirdly*, in the ventral surface of the ilium behind the ilio-pectineal line, and in the ventral surface of the scapula behind the supra- or pre-spinal ridge: *fourthly*, in the inferior edge of the iliac blade just above the acetabular surface and in the inferior edge of the scapular spine just above the glenoid surface; *fifthly*, in the posterior or sciatic edge of the ilium near the acetabulum, and in the posterior edge of the scapula near the glenoid cavity. In the lower animals the nutritious foramina are less constant than in man; but when they appear they are in or near one or other of the situations indicated.

The origin of the *rectus femoris*, from the anterior border of the ilium, and of its homologue the long portion of the *triceps* from the hinder border of the scapula, may be esteemed an argument in favour of the correspondence of these two borders, and so of the rotation of the scapula and ilium in opposite directions. But it must be remembered that the triceps arises from the outer surface of the scapula as well as from the

hinder border, and that the rectus extends from the anterior border of the ilium upon its outer surface above the acetabulum. The origin therefore of the two may be traced to corresponding points upon the external or dorsal aspects of their respective bones; and the one has been turned backwards upon the hinder border of the scapula, while the other has been turned forwards upon the anterior border of the ilium, in consequence of the rotation of the extensor surfaces of the limbs in those directions[1]. This difficulty becomes therefore an argument in favour of the view that the rotation of the parts of the limbs that are free from the body is not accompanied by a corresponding rotation of the parts lying in the visceral wall.

An important difference between the two limbs in mammals, which has a material effect upon the inferior components of the girdles, is to be found in the position of the limbs, or rather of the proximal components of the limbs, with regard to the respective girdles. The hind limb impinges upon the pelvis *laterally*. The direction of forces from it to the pelvis is consequently *in*wards as well as upwards; and this is associated, as a general rule, with the completion of the bony arch beneath which is effected by means of the great development of the ischium and os pubis, and the meeting of the pubic and perhaps the ischiatic bones of the two sides at the symphysis. The fore-limb including the humerus in mammals, excepting monotremes, is placed *beneath*, that is, in a line with the scapula, and the forces are consequently directed from it to the scapula more vertically than in the case of the hind-limb. The lower elements of the girdle are accordingly comparatively abortive, and do not approach the middle line. In monotremes, however, as well in the inferior classes, the fore-limbs are more sprawling, the humerus runs out almost horizontally from the trunk, the glenoid cavity is more lateralized and the direction of forces from the limb is more *in*wards. Hence the lower elements of the girdle acquire a development more or less corresponding with those of the pelvis, and abut upon one another or upon the sternum.

Another, but less important difference, to some extent

[1] In Manis the *triceps* arises from the whole length of the spine of the scapula, as well as from the hinder border. *Journal of Anat.* iv. 38.

associated with the preceding, is a rotation in opposite directions in the two girdles, which may be connected with the rotation in opposite directions in the two limbs already referred to. It must, however, be clearly understood that this is altogether different from the rotation of the ilium and scapula upon their longitudinal or vertical axes which I have been arguing against. The rotation to which I now refer is one upon a transverse axis drawn through the two acetabula in the case of the pelvis, and through the two glenoid cavities in the case of the shoulder[1].

In what we may suppose to be the primitive condition, as illustrated by the Chameleon and many other reptiles, the pelvic and scapular girdles are almost vertical. The nearly straight and flat ilium and scapula descend to the articular spaces whence the two inferior elements of either girdle pass inwards and downwards enclosing perhaps a space between them. The arm and thigh-bones run out nearly horizontally so that the axes of the two arm-bones, if prolonged inwards, would meet and form one horizontal straight line passing through both glenoid cavities and constituting the axis of the rotation of the scapula to which I refer. In like manner the axis of pelvic rotation is the axes of the two thigh-bones traversing the acetabula and meeting in the middle line. Now, the developmental rotation of the limbs takes place upon these axes, and is accompanied, or is often accompanied, by a corresponding rotation of the girdles upon the same axes. Thus when the hind-limb rotates so that the upper or extensor surface turns forwards, and the under or flexor surface backwards, there is a rotation, not of the ilium upon its vertical axis, but of the whole pelvis, turning the upper edge of the ilium forwards and the hinder edge of the ischium backwards. Also when the fore-limb rotates, so that its upper or extensor surface turns backwards, and its under or flexor surface turns forwards, the rotation affects, not the scapula upon a vertical axis, but the whole girdle upon a horizontal axis, turning the upper edge of the scapula backward and the coracoid forwards.

I should observe, however, that this turning of the girdles

[1] It is a change of like kind with that which brings the pelvic bones of the fish into a horizontal position from the vertical direction of the interspinous bones (p. 63). It is however less in extent; and in the shoulder girdle usually, and in the pelvic girdle sometimes, is in an opposite direction to that in the fish.

upon a transverse axis is very uncertain, and does not always correspond in amount or even in direction with that of the limbs. The pelvis, for instance, in rodents, in birds and the Frog undergoes very nearly a quarter turn; and the ischium is in the Beaver thrown nearly, and in the Great Anteater quite, into contact with the caudal vertebræ, and in Aï it is anchylosed with them; and in this animal and most birds, it sends forwards a process which nearly or quite blends with the hinder margin of the ilium, and converts the sacro-sciatic notch into a hole. In Pteropus the two ischiatic bones are united together in the middle line behind the tail. In the Kangaroo the turn hardly takes place at all; and in most saurians the pelvis is turned in a contrary direction, the ilium being slanted backwards. In the shoulder girdle the rotation is usually slight. In the through-bred Horse it is as marked as in any instance that occurs to me. Some of the elements are however not uncommonly slanted, *i.e.*, grow out from the glenoid area in the direction indicated without the other or others being much altered. Thus in the bird the scapula is slanted backwards, although the coracoid maintains its primitive direction inwards; and in all the mammals in which the humerus is directed downwards from the shoulder, the inferior elements of the girdle, concentrated in the small short coracoid, are directed forwards, although the scapular blade is but little altered from its primitive upward direction. It is here worthy of remark that as the backward projecting ischium of Aï and some birds comes into contact with, and unites with the backward growing hinder or sciatic spine of the ilium, so in Aï does the forward projecting coracoid unite with the forward growing anterior or prespinal edge of the scapula and encloses the supra-scapular hole.

A word or two respecting the clavicle. Imbedded in the superficial stratum of muscles and stretching across from the acromion or overhanging projection at the inferior extremity of the spine, *i.e.*, the external ridge, of the scapula towards the median line, where it unites with its fellow by anchylosis or by ligament, and perhaps impinges upon the sternum, it seems to answer to the tendinous fibres called Poupart's ligament which, lying in or forming part of the superficial muscular stratum, stretch across from the anterior iliac spine, or over-

hanging projection, of the external ridge of the ilium, towards the median line. There they not only impinge upon and are implanted into the pubic bone, but some of the fibres are commonly united in the median line with those of the opposite side. May not the interclavicle or episternum, which in monotremes and saurians subtends the clavicles, and, extending beneath the sternum, gives origin on its sides to the *pectorals*, be regarded as an ossification of tissue homologous to that which subtends Poupart's ligaments and, extending beneath the symphysis pubis, gives origin on either side to the fibres of the *gracilis*. Further, are not both clavicle and Poupart's ligament serially homologous with the intermuscular bones in the blended obliqui externi and recti of saurians where they occupy a plane underlying, that is, superficial to, the costal cartilages.

I conclude therefore that the following parts are respectively homologous. The *pre-spinal ridge* of the scapula, which forms the floor of the pre-spinal fossa, and the *linea ileo-pectinea* of the ilium:—the *spine* of the scapula with the *acromion*, and the *fore* part of the *blade* and *crest* of the ilium with its anterior *spine* or *angle*:—the *post-spinal* part of the scapula, which forms the floor of the post-spinal fossa, and the *hinder* part of the *blade* and *crest* of the ilium; the *posterior angle* of the scapula corresponding with the *posterior 'spine'* or *angle* of the ilium:—the *hinder border* of the scapula, and the *hinder* or sciatic *border* of the ilium:—the *inner* or ventral surface of the scapula, and the *inner* or true pelvic surface of the ilium, including the surface for articulation with the sacrum:—the *coracoid*, which in reptiles divides into coracoid and precoracoid with an intervening *fenestra*, and the *ischiatic* and *pubic bones* with the *obturator* hole:—the *clavicle*, and *Poupart's ligament*:—the *interclavicle*, and the *fibrous tissue* beneath the symphysis pubis.

In order to obtain a correct apprehension of the relations of the muscles in the two limbs, it is necessary to bear in mind that the shoulder and pelvic girdles are developed in and form parts of the descending or visceral plates of the embryo, a half of each girdle on each side, that they lie in the innermost stratum of those plates and are connected with the several strata of muscles in them; and that the limbs, as they emerge from the

ventro-lateral regions of those plates, carry out with them prolongations of their muscles which extend to greater or less distance and acquire attachment to the bony framework of the limbs. These muscles may be divided into a dorsal and a ventral series which converge respectively from the dorsal and the ventral aspects of the trunk upon the dorsal and the ventral aspects of the limbs, and form an external or superficial sheet upon them. A deeper sheet is formed by the muscles passing from the half-girdle of each side to its limb. These also constitute a dorsal and a ventral series according to their connection with the part of the girdle above or beneath the point from which the limb springs.

In the primitive state the extensor aspect of each limb is dorsal, and the flexor aspect is ventral; and the dorsal muscles both from the trunk and the girdles pass upon the extensor or dorsal aspect of the limbs, and the ventral muscles both from the trunk and the girdles pass upon the flexor or ventral aspect of the limbs. In short, the several layers from the skin inwards are continuations of the several layers of the embryonic laminæ and they are continued dorsally, ventrally, anteriorly and posteriorly upon the corresponding aspects of the limbs.

Thus far the matter is simple enough; and it is on the whole easy to refer the several muscles to their respective dorsal and ventral groups both in the trunk and the girdle series. Complications however arise from various causes which create some difficulties, especially in the sub-division of the several groups and in the comparison of these subdivisions in the two limbs.

First, the members of the dorsal and ventral series do not always rigidly adhere to their respective aspects of the limb. The lateral or marginal muscles especially may overlap their appropriate margins and extend from a dorsal to a ventral aspect. Thus the *latissimus dorsi,* which obviously belongs to the dorsal series and often blends with the triceps extensor cubiti, is not unfrequently continued on to the flexor aspect of the forearm: in Manis[1] it is continued into the *flexor digitorum;* and in Unau[2] the *tibialis anticus* is continued into the *flexor digitorum pedis.*

[1] *Journal of Anat.* IV. 35.

[2] *Journal of Anat.* IV. 67.

Secondly, a muscle may be attached higher or lower, or near to one or other margin of the dorsal or ventral aspect of its bone. The *latissimus dorsi,* for instance, in the bird passes, on the radial side of the humeral part of the triceps, to the radial edge of the humerus; in saurians it passes between the divisions of the triceps to near the middle of the dorsal aspect of the bone: whereas in mammals it passes on the ulnar side of the triceps to the ulnar margin of the bone. True, this kind of variation does not often occur to any great extent; but it is not always easy to make sure respecting it; and where it does occur it throws much doubt upon homological arrangement.

Thirdly, although in the distal segments of the limbs the dorsal and ventral surfaces, as well as the radial or tibial and the ulnar or fibular margins, are pretty clearly defined, and the distinction between the dorsal and the ventral groups of muscles is comparatively easy, yet in the proximal segments, where there is only one bone in each limb, this is not the case, especially in the middle and towards the upper ends of the segments. In many reptiles and birds, and in monotremes, it is true, the upper end of the humerus is flattened, and the dorsal and ventral surfaces are separated by anterior and posterior ridges which terminate in the anterior or radial and the posterior or ulnar projections or tubercles; but in other animals the dorsal or extensor surface is increased at the expense of the ventral or flexor surface. The marginal lines and tubercles are pressed or folded to the flexor side and come almost into apposition, leaving between them, it may be, little more than the interspace for the biceps tendon. It is difficult in some such cases to define how much appertains to the dorsal and how much to the ventral surface; and the difficulty is increased by the fact of the muscular attachments overstepping what may morphologically be called their proper limits. In the case of the femur we rarely meet with so equal a division into dorsal and ventral aspects as is seen in the humerus of the animals just mentioned. Here too the extensor is increased at the expense of the flexor surface, which is partly in consequence of the flexor muscles of the leg having little or no connection with the femur: the lateral margins of the shaft are folded almost into contact in the linea aspera, and sometimes, as in saurians,

the lateral tubercles are blended into one ventrally-placed spine.

Fourthly, the rotation of the fore and hind limbs in opposite directions necessarily tends to increase the confusion. It does so, not simply by reversing the relative position of the muscles, but, I think, also by impressing in some instances an opposite developmental tendency upon the muscles of the two limbs and causing them to be directed in each towards that margin or that tubercle which will be most appropriate to their action in the final position of the limb. This seems to me to be an explanation of the fact which has been the source of so much embarrassment to homologists, and which indeed precludes an exact serially homological comparison of the fore and hind limbs, viz., that the muscles from the dorsal aspect of the scapula pass to the radial tubercle of the humerus, while those from the dorsal aspect of the ilium pass to the fibular tubercle of the femur. Those tubercles in the two limbs, though homologically different, yet in size, in position, in function, and to some extent also in muscular relations, are made to answer to one another. That the course of muscular transformation in the embryonic plasma should be thus conformed to the future requirements of the two limbs is no more than other modifications would lead us to expect; especially when we find the dispositions just referred to, of the latissimus dorsi in birds and saurians, and of the tibialis anticus in Manis, presenting instances of a like kind in corresponding limbs.

Fifthly, more numerous are the infringements of serial homological order presented by the blood-vessels and nerves passing to the several muscles in the two limbs. The blood-vessels are perhaps the most conformable of animal structures, which is no more than would be expected from their mode of formation and their disposition, and they give us very little help in our present task. From the nerves, more of definiteness in arrangement and tenacity of serial homology is to be expected, than from the blood-vessels. Still, when we mark the differences in the disposition of the nerves in the two limbs, and the intricate manner in which the nerves passing to the limbs are respectively blended in the cervical and the lumbo-sciatic plexuses, our confidence in any readily available assistance from

this quarter in cases of difficulty, in the present state of our knowledge, is very much shaken. Further investigation and more accurate dissection may exhibit more harmony in the disposition of the nerves in the two limbs than we can at present trace, and may not improbably lead to a modification of some of the views to which we are now led.

I will now endeavour to make a comparison of the muscles about the shoulder with those about the hip, in accordance with the principles I have laid down; and first, of the muscles passing from the trunk to the limbs. These may be arranged into dorsal, ventral, anterior and posterior. The last two might be described as lateral muscles, being derivatives from the great lateral system of muscles which is so fully developed in the fish.

The DORSAL trunk-muscles pass from the vertebral spines to the limbs, and consist of a superficial and a deep layer.

The superficial layer is composed of the *trapezius*, the *latissimus dorsi* and the *gluteus maximus*. These form a nearly continuous series; and their several parts, that is to say, their several component portions passing from the several vertebral spines, may be regarded, generally speaking, as serially homologous[1]. Each of them is therefore, in this sense, serially homologous with the others; and the attachment of the *latissimus dorsi* to the crest of the ilium is a repetition of the attachment of the *trapezius* to the scapula. The similarity, however, between the *latissimus dorsi* and the *gluteus maximus* is very evident. The former passes over the hinder angle of the scapula, deriving fibres from it, lies on the ulnar side of triceps, and is implanted into the dorsal aspect of the humerus usually near the ulnar ridge. It is often blended, to some extent, by means of connecting slips with the triceps; and prolongations

[1] I use the phrase 'serially homologous' in this and some other places to indicate not merely the corresponding muscles in the upper and lower limbs, but also the muscular bundles arising from corresponding parts of the vertebræ in different regions of the column. In this sense the several bundles of the trapezius are serially homologous with one another and with the several bundles of the latissimus dorsi and the gluteus. The destinations of the collective bundles of the latissimus dorsi and of the gluteus indicate a more special serial homology between these two muscles than between either of them and the trapezius. The whole are in a general way serially homologous, whereas some of them only are specially so.

of it occasionally pass to the ulnar condyle, or on to the flexor aspect of the forearm, being traceable as far as the wrist[1]. The *gluteus* in like manner frequently derives origin from the posterior angle of the ilium, lies on the fibular side of the quadriceps, and is implanted into the dorsal aspect of the femur usually, near to the fibular line. It sends a fascial expansion over the quadriceps extensor, and is frequently continued on to the flexor aspect of the leg chiefly on the fibular side as far as the ankle.

The deeper layer of the dorsal series, which is probably a segmentation from the trapezius, consists of the *rhomboids*, to which are sometimes added the *masto-scapular* and the *occipito scapular*[2]. These have no distinct representatives in the hind-limb.

The VENTRAL trunk-muscles to the fore-limb are the *Pectorals*. They pass on the radial side of the flexors of the forearm, and are attached upon the ventral aspect of the humerus near the radial line, which is here projected into what is called the pectoral crest. The superficial stratum, arising along the ventral mesial line from the sternum and the tissue superficial to it, from the episternum and clavicle, when they are present, descends lower than the rest of the muscle, and is not unfrequently continued upon the radial side of the flexor surface of the forearm. It is represented in the hind-limb by the *gracilis* which, arising from the symphysis pubis and the tissue superficial to it, extends, upon the flexor surface of the leg, often to the ankle and to the

[1] In the Frog the *latissimus dorsi* joins the hinder edge of the *dorsalis scapulæ*, in which are blended the *infra-spinatus* and *teres minor* and *major*, and its tendon passes with it on the radial side of the *triceps* to near the radial edge of the humerus just beneath the deltoid. In the bird (Owl) it arises in two separate small slips, one above the other, which pass together, between the scapular and humeral portions of the *triceps*, to the dorsal aspect of the pectoral crest just beneath the *deltoid;* it is separate from the *teres major*, which is large and runs to the dorsal aspect of the ulnar tubercle. In the saurian (Scinc) it runs between the two scapular origins of the *triceps*, then between the two humeral origins, to near the middle of the dorsal aspect of the humerus : the teres major is separate from it and disposed as in the bird. In the two-toed Ant-eater it crosses beneath the flexor aspect of the humerus to the radial edge beneath the pectoralis major (*Journal of Anat.* IV. 34, see there remarks on the disposition of this muscle).

Indeed, both this muscle and the *gluteus maximus* are exceedingly variable in size, in the range of origin and insertion, and in the extent of limb covered by them. See disposition of Gluteus in Manis, Vol. IV. 52.

[2] The *cleido-occipital* and *cervico-humeral* are also occasional segmentations from the trapezius, but do not belong to the deeper layer.

inner edge of the tibia. Deeper strata of the pectoral arising from the ribs cross the superficial fibres and take a more upward direction towards the upper part of the pectoral crest, and may extend to the coracoid or the clavicle. These, or parts of them, are sometimes segmented as distinct muscles—the *pectoralis minor*, and the *subclavius*—The latter, as shewn by Prof. Rolleston, in the bird passes on over the coracoid to the humerus, constituting the *pectoralis secundus*. It still conforms to the disposition of the members of the ventral group in being inserted on the ventral aspect of the radial tubercle. These deeper strata do not appear to have any distinct representative in the hind-limb. It may be that they are there merged in the adductor series.

The POSTERIOR trunk muscles passing to the fore-limb are the *serratus magnus*, arising from the ribs behind and beneath the scapula, and inserted into the hinder or upper border of the bone, and the *sterno-coracoid* which passes from the deeper surface of the sternum to the deeper surface of the coracoid in the animals in which the coracoid and sternum are in contact. The brachial vessels and nerves pass between these two muscles.

The ANTERIOR trunk muscles are the *levator scapulæ*[1] and *omohyoid*, which are inserted into the anterior border of the scapula[2].

The fibres of the *quadratus lumborum* which pass from the transverse lumbar processes to the hinder part of the anterior margin of the ilium are probably the serial homologues of the *levator scapulæ*. The other lateral scapular trunk-muscles do not appear to be represented by any distinct pelvic trunk-muscles; but there are pelvic trunk-muscles—the *sacro-lumbalis*, *ischio-coccygeus*, &c., which have no distinct representatives in connection with the scapula.

There remain the *psoas* muscles, the relations of which to the quadratus lumborum and iliacus internus indicate that their representatives if present would appear anterior and internal to

[1] The *levator scapulæ* and the *serratus* are often continuous, so that the two might be described as one muscle lying before, behind, and beneath the scapula.

[2] It is worthy of remark that in Echidna the omohyoid preserves its usual relations, being inserted beneath the supra-spinatus into a faint ridge which represents the anterior border of the scapula, and resembles the ilio-pectineal line of the human ilium.

the levator scapulæ and the supra-spinatus. The *cervico-humeral* does not usually answer to the conditions; but it is extremely interesting to note that in Phoca (Vol. II. 299) one portion of this muscle extends from the transverse process of the atlas to the anterior angle of the scapula, and overlaps the supra-spinatus, thus presenting very close homological relations to the *psoas parvus;* and in that and some other animals an extension of the *levator scapulæ* into the fascia over the *supra-spinatus* remind us of the relations of the *psoas magnus* to the *iliacus internus.*

We come now to the muscles passing from the shoulder and the pelvic girdles to the humerus and the femur. They may be divided into dorsal and ventral, anterior and posterior, which are disposed accordingly upon the dorsal and ventral, the anterior and posterior aspects of the shoulder-girdle and humerus, and the pelvic girdle and femur.

The DORSAL series of girdle-muscles in the fore-limb consists of the *deltoid*, *infra-spinatus* and *teres minor.* The *deltoid* passes from the spine of the scapula, the acromion, and the outer part of the clavicle to the extensor or dorsal aspect of the radial line of the humerus, nearly opposite to the attachment of the pectoral. It sometimes (Orycteropus) extends with the flexor of the forearm to the radius, and in Manis it joins the *supinator radii longus*[1]. It seems to be represented by the *sartorius,* which arises from the anterior iliac spine often extending upon Poupart's ligament, and is inserted either into the dorsal aspect of the tibial line of the femur internal to the vastus internus, or passes down to the tibia, meeting the gracilis much as the deltoid meets the pectoral. I may observe that the occasional

[1] *Journal of Anat.* IV. 36 and 40. The *extensor plicæ alaris* of the bird may also be regarded as a derivation from the deltoid to the supinator and the radial edge of the wing. The clavicular and the scapular parts of the deltoid are not unfrequently separate; and the latter sometimes blends with the triceps (see Pteropus, *Journal of Anat.* III. 305). This part may be represented by the *tensor vaginæ femoris*, which is sometimes inserted into the dorsal aspect of the femur.

In Manis, the *sartorius*, *tensor vaginæ femoris*, and *gluteus maximus* are continuous; and in that animal the *supinator longus* extends up to the spine of the scapula, displacing the fore part of the *deltoid*, reminding us of the connection of the supinator with the deltoid in the bird, and suggesting the serial homological relation of that connecting portion and of the *extensor plicæ alaris* with the sartorius. See Disposition of Sartorius, in Vol. IV. 55.

extension of the *gracilis* upon the inner, and of the *sartorius* upon the outer part of Poupart's ligament, remind us of the extension of their homologues—the *pectoralis major*, and the *deltoid*—upon the inner and outer parts of the clavicle. The relation thus established between the *gracilis* and *sartorius* with the *external oblique*, resembling that of the *pectoral* and *deltoid* with the *cleido-mastoid* and *trapezius*, and the occasional continuity of the *sartorius* and *tensor vaginæ femoris* with the *gluteus magnus*, suggest that all these muscles appertain to, and are segmented from, one continuous muscular stratum passing from the anterior and posterior median lines of the trunk upon the limbs[1].

The *infra-spinatus* and *teres minor* are represented by the *gluteus medius and minimus*. The segmentation in each instance is often incomplete. The two in the fore-limb are sometimes formed into one *dorsalis scapulæ*. The difficulty in the comparison of these muscles caused by those in the fore-limb passing to the radial tubercle, while those in the hind-limb pass to the ulnar trochanter, has already been alluded to, and I hope, removed.

The *teres major* passes from the hinder angle of the scapular on the ulnar side of the triceps, to the ulnar edge of the humerus, and is the POSTERIOR girdle-muscle of the fore-limb. It is commonly placed upon the dorsal aspect of the angle though it sometimes lies upon the ventral aspect[2]; and it sometimes passes on to the dorsal aspect of the humerus. It is often related in its whole length to the latissimus dorsi, yet is sometimes quite separate from it. It is sometimes (Frog) apparently blended with the infra-spinatus and teres minor in the dorsalis scapulæ; though when separate its nervous supply is from a different source (the subscapular). Its general relations therefore give it rather a dorsal character. This makes me hesitate to compare it with the *pyriformis* in the hind-limb, which, arising slightly from the ventral aspect of the posterior spine of the ilium, and largely from the same aspect of the transverse processes of the sacral and caudal vertebræ, and

[1] See remarks in paper on Anatomy of Orycteropus in Vol. II. 298.

[2] In Manis I found it arising from the hinder border and inner surface of the scapula internal to the triceps. *Journal of Anat.* IV. 36; also in Orycteropus, II. 300.

inserted into the ventral aspect of the fibular trochanter, has a more ventral situation. Yet the position of the two muscles on the whole, their relations to the hinder borders of the scapula and the ilium, to the great vessels and nerves of the two limbs (these passing over the inner aspect of the muscle in each instance) and to the circumflex and dorsalis scapulæ vessels in the one case, and the glutæal vessels in the other (these vessels crossing in front of the respective muscles and passing between them and the borders of the scapulæ and ilium)—added to the fact that the pyriformis is often absent, or blended with the gluteus medius, just as the teres major is often blended with the infra-spinatus—indicate a correspondence that cannot be overlooked[1].

The ANTERIOR girdle-muscles are the *supra-* or *pre-spinatus* in the fore-limb and the *iliacus internus* in the hind-limb. The former passes from the pre-spinal fossa of the scapula, over the fore part of the coracoid and shoulder-joint, to the edge of the radial tubercle of the humerus; and the latter passes from the pre-spinal fossa of the ilium, over the precoracoid and fore part of the hip joint, to the edge of the tibial trochanter of the femur[2]. In the fore-limb of the saurian the *prespinatus* extends upon the broad precoracoid, and in the hind of the same animal, the *iliacus internus* extends upon the broad pubic bone, or pre-ischium.

The VENTRAL girdle-muscles pass from the lower elements of the girdles, the coracoid and the ischiatics, to the ventral aspect, and chiefly to the ulnar and fibular sides of the humerus and femur. They are formed chiefly in the fore-limb by the *coraco-brachials* and, in the hind limb, by the *adductors*, including the *pectineus*, and the *external obturator*. All these vary in size and number in accordance with the varying development of the bones from which they spring[3], and

[1] The remarkable muscle in saurians called *Pyriformis*, which arises by a long thick fleshy belly from the under surface of the transverse processes of several caudal vertebræ, and is inserted by a strong tendon on the tibial side of the single ventrally placed trochanter, and which detaches at right angles a tendon to the fibula, presents strong claim to its name, and is probably either the homologue or the serial homologue of the pyriformis of mammals.

[2] The *iliacus* frequently extends lower down on the femur, and the *supra-spinatus* occasionally (Phoca) extends lower down on the humerus.

[3] In Cyclothurus and Manis where there is no appreciable coracoid there is no coraco-brachialis.

are accordingly more numerous and larger in the hind-limb than in the fore-limb, and in the fore-limb they are larger in ovipara and monotremes than in ordinary mammals. When the coraco-brachials are extensively disposed along the humerus, they are pierced by the brachial artery, passing from the extensor to the flexor aspect of the limb; just as in the hind-limb the adductors are pierced by the femoral artery passing from the front of the thigh to the ham[1].

These remarks apply to the coraco-brachials and adductors which arise from the *exterior* of the coracoids and pub-ischiatic. But there coraco-brachials which arise from the *internal* surface of the coracoids in the animals where those bones are prolonged to the sternum, and which either join the external coraco-brachials, and pass with them down the humerus; or which ascend to the ulnar tubercle of the humerus[2]. There is often—and that is the case in saurians—one of each, that is to say, there is an *inferior internal coraco-brachialis*, which passes from the internal surface of the coracoid to the shaft of the humerus, and a *superior internal coraco-brachialis* which passes from the inner surface of the coracoid to the ulnar tubercle of the humerus. The latter is the larger, and is closely connected, or continuous, with the *subscapularis*. I apprehend that these internal coraco-brachials (one or both) are represented by the internal ischio-femoral (the *obturator internus* or the lower part of it) which passes from the internal surface of the ischio-pubic bone and the obturator ligament to the ventral aspect of the fibular trochanter. The upper bundles of the *obturator* which are expanded upon the ventral surface of the ilium, beneath the ilio-pectineal line, appear to correspond with the *subscapularis*. The *quadratus femoris* is merely a segment of the *adductor magnus;* and if any special homologues of the *gemelli* are to be sought, it must be in the coraco-brachial groups.

[1] There are in many animals two external coraco-brachials, one passing to the internal condyle and lower part of the humerus, and the other inserted higher up, beneath the ulnar tubercle. The vessels pass between the two.

[2] This upper internal coracoid is described by Mr Mivart in his excellent paper on the Echidna (*Linn. Trans.* xxv. 385). I can bear witness to the correctness of his description of this and most of the other muscles of that animal. The coraco-brachial of the bird belongs to this internal set, whereas the so-called *pectoralis tertius*, shewn by Prof. Rolleston to be a coraco-brachial, belongs to the external set.

EXPLANATION OF PLATE III.

Fig. 1. The outer surface of the pelvis of an Echidna (natural size): 2. the same of a Beaver (one half of the natural size): 3. the same of a Hare (natural size): 4. the same of Pteropus. In all these *il.* is the surface for the iliacus muscle, and *gl.* that for the gluteal muscles.

Fig. 5. The outer surface of the scapula of a Horse (one-fifth the natural size); *s. sp.* the surface for the supra-spinatus muscle; *i. sp.* the surface for the infra-spinatus muscle.

Fig. 6. The outer surface of one side of the shoulder girdle of a Chameleon (nat. size).

Fig. 7. The outer surface of one side of the pelvic girdle of a Chameleon.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig 6.

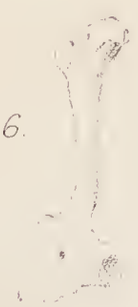

Fig. 7.